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<https://doi.org/10.1038/nature02286>

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Received 12 August; accepted 14 November 2003; doi:10.1038/nature02231.

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Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements We thank J. Ni, R. Aster, and the rest of the RISTRA team for the use of their data set, and we acknowledge all who have contributed to the PASSCAL arrays and IRIS DMC. We also thank H. Gilbert for providing receiver-function profiles. Reviews from D. Anderson, P. Asimow, T. Ahrens, B. Savage and M. Simons also helped to clarify early versions of this paper. We benefited from discussions with H. Gilbert, D. Anderson, H. Kanamori, Y. Tan, S. Ni and M. Gurnis. We thank L. Zhu for sharing his receiver function modelling code. This study was supported by the NSF and is a contribution to Division of Geological and Planetary Science, Caltech.

Competing interests statement The authors declare that they have no competing financial interests.

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Mangroves enhance the biomass of coral reef fish communities in the Caribbean

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Mangrove forests are one of the world's most threatened tropical ecosystems with global loss exceeding 35% (ref. 1). Juvenile coral reef fish often inhabit mangroves^{2–5}, but the importance of these nurseries to reef fish population dynamics has not been quantified. Indeed, mangroves might be expected to have negligible influence on reef fish communities: juvenile fish can inhabit alternative habitats and fish populations may be regulated by other limiting factors such as larval supply or fishing⁶. Here we show that mangroves are unexpectedly important, serving as an intermediate nursery habitat that may increase the survivorship of young fish. Mangroves in the Caribbean strongly influence the community structure of fish on neighbouring coral reefs. In addition, the biomass of several commercially important species is more than doubled when adult habitat is connected to mangroves. The largest herbivorous fish in the Atlantic, *Scarus guacamaia*, has a functional dependency on mangroves and has suffered local extinction after mangrove removal. Current rates of mangrove deforestation are likely to have severe deleterious consequences for the ecosystem function, fisheries productivity and resilience of reefs. Conservation efforts should protect connected corridors of mangroves, seagrass beds and coral reefs.

The Mesoamerican reef system of Belize and Mexico provides a unique experimental setting that has allowed us to isolate the importance of mangroves to coral reef fish. Three atolls have virtually no, or extremely limited, mangrove cover. As migrations from the nearest mangrove resource, across 10–25 km of open ocean with depths exceeding 2,000 m, are likely to be insignificant for demersal reef species⁷, we can assume that adult fish must have used nursery habitats, such as seagrass, on the atolls. These reef systems provide three 'scarce mangrove' treatments, in which the mean mangrove perimeter is only 3.9 km within an area the size of Glovers Reef (228 km²).

Uniquely in the region, Belize also possesses a mangrove-dominated atoll and extensive offshore mangrove islands at the edge of a barrier reef. The offshore barrier reef is separated from the mainland by a channel that is roughly 15-km wide, and sediment cores show that there is little (<1%) connectivity with the mainland⁸. The existence of these offshore, 'rich mangrove' atoll and barrier reef areas allowed us to contrast the fish communities of three mangrove-scarce reef systems with those of three mangrove-rich systems (one atoll and two areas of the barrier reef). The

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mangrove perimeters in the mangrove-rich treatments were, on average, almost fifty times greater (185 km). Notably, with the exception of mangrove, for which habitat availability differed significantly between the mangrove-rich and mangrove-scarce treatments (Mann–Whitney test, $P < 0.05$), the area of reef and lagoon habitats was highly consistent among all six systems (see Fig. 1a and Supplementary Information for details of the habitat characteristics at the study sites). There was no latitudinal bias in the locations of treatments (Fig. 1a), and all shared a common biogeographic province⁹. More than 100,000 fish from 164 species were surveyed visually.

The structure of reef fish communities in outer *Montastraea* reefs differed markedly between mangrove-rich and mangrove-scarce sites (Fig. 1b). The magnitude of such differences was tested by nested ANOSIM¹⁰, where the output statistic (R) equals unity when a factor, such as mangrove extent, divides the data into tight, non-overlapping groups. Given the possibility that mangroves are a redundant nursery habitat and only one of a range of potential limiting factors, we were surprised to find that mangrove extent was a dominant factor structuring reef fish communities. Mangrove

extent not only explained a significant component of community structure, but it usually exceeded the influence of reef systems ($R_{\text{mangrove}} = 0.74, P < 0.05; R_{\text{reef}} = 0.49, P < 0.001$). These results were highly robust to the units used and the aspect of fish community structure under analysis (see Supplementary Information). The factor mangrove extent even partly explained patterns of community structure in reef fishes that can be considered as obligate reef species not occupying lagoonal nurseries ($R_{\text{mangrove}} = 0.59, P < 0.05; R_{\text{reef}} = 0.66, P < 0.001$). This suggests that interactions within the fish community are strong enough that mangrove deforestation will also affect populations of obligate reef species.

Studies elsewhere in the Caribbean suggest that four reef fish species are heavily dependent on lagoonal nurseries, although, unlike in our study, the importance of mangroves was not isolated¹¹. These species were the striped parrotfish (*Scarus iserti*), bluestriped grunt (*Haemulon sciurus*) and the commercially important yellowtail (*Ocyurus chrysurus*) and schoolmaster (*Lutjanus apodus*) snap-

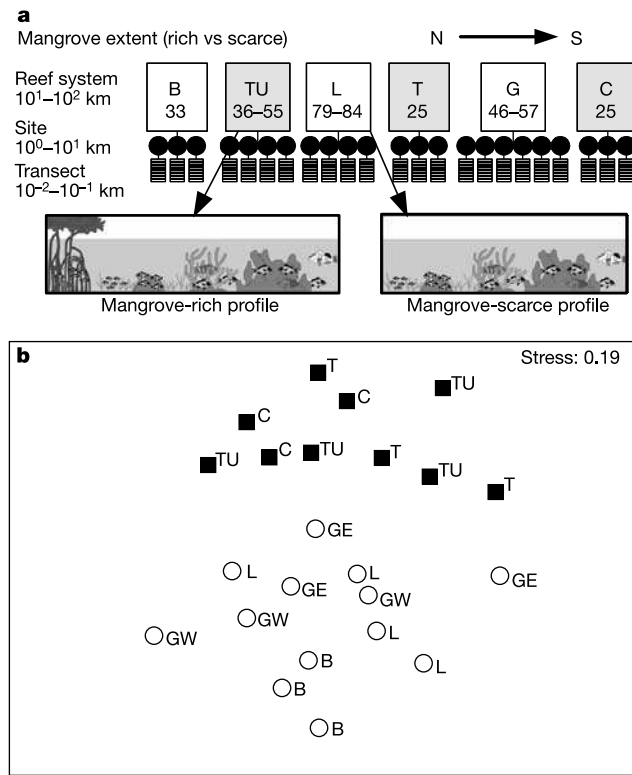


Figure 1 Spatial patterns of sampling and community structure in reef fish. **a**, Study design showing nested scales of sampling, latitudinal sequence and the distance in kilometres of reef systems from the mainland. Boxes denote mangrove-rich (shaded) and mangrove-scarce (open) systems. Habitats included mangrove prop roots (*Rhizophora mangle*), seagrass beds, patch reefs, shallow forereefs (depth, 2–5 m) and *Montastraea* reefs (depth, 9–12 m). *Montastraea* reefs were chosen because they have the greatest fish density and diversity of all outer reef habitats. **b**, Multidimensional scaling ordination¹⁰ of community structure (measured by the Bray–Curtis dissimilarity coefficient) at each site. Species were included that occupied lagoon habitats during at least one life stage (juvenile, pre-adult and adult) but excluded carangids, large serranids and large lutjanids. Density data were log-transformed. Squares represent mangrove-rich and circles mangrove-scarce sites. The reef systems are as follows: B, Banco Chinchorro; TU, Turneffe Islands; L, Lighthouse Reef; T, Tobacco Cay; G, Glovers Reef (GW and GE denoting western and eastern sides, respectively); C, Curlew Bank.

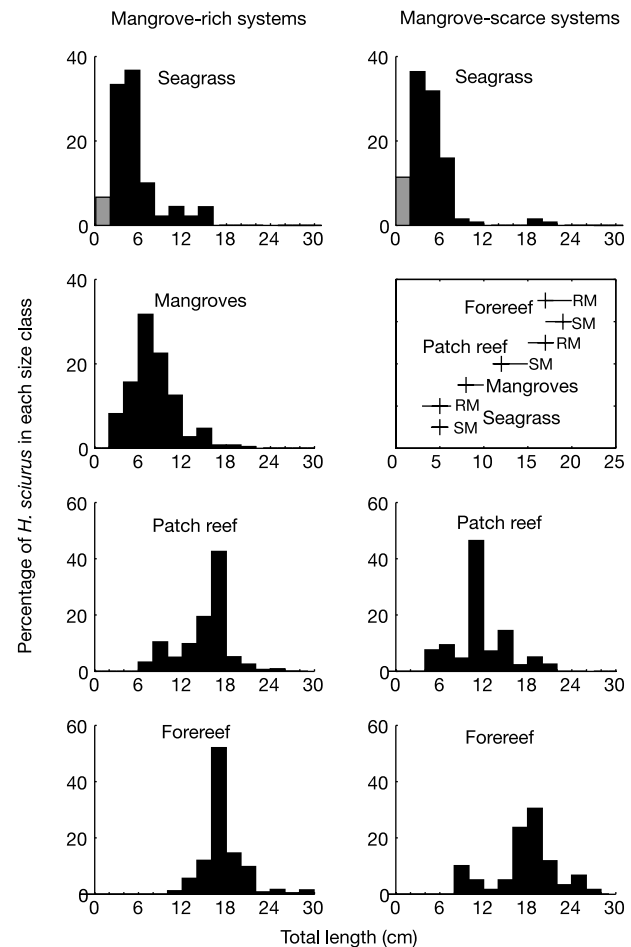


Figure 2 Ontogenetic patterns of habitat use in *H. sciurus*. Shifts in median length among seagrass, mangrove, patch reef and forereef are all significant within each system (Kruskal–Wallis test with Mann–Whitney comparisons among medians, $P < 0.0002$). Intersystem comparisons show that median lengths and densities between seagrass systems do not differ significantly (Mann–Whitney, $P > 0.05$), whereas lengths on patch reefs are significantly greater in mangrove-rich systems ($P < 0.05$). Data are pooled from all systems. Sizes in grey indicate that species identification was tentative at this size (but these difficulties do not affect our conclusions). Inset shows median and interquartile size range of *H. sciurus*, and shows that the gap in median fish length between seagrass and patch reefs is greater in systems with rich mangrove (RM) than scarce mangrove (SM).

pers. We therefore examined the biomass of these species, but we included two additional species that were often seen in the mangroves as juveniles: the French grunt (*Haemulon flavolineatum*) and white grunt (*Haemulon plumieri*). Although none of the species was absent from reefs in mangrove-scarce systems, their biomass was significantly enhanced in at least one reef habitat in mangrove-rich systems (Table 1). The magnitude and pattern of biomass enrichment differed among species (Table 1). *H. sciurus* benefited most strongly from mangroves: biomass on patch reefs in mangrove-rich systems was over 25 times higher than that in mangrove-scarce systems. The biomass of *O. chrysurus* doubled when its preferred *Montastraea* habitat was adjacent to rich mangroves (Table 1). A similar analysis for *S. iserti* showed a 42% biomass increase on the *Montastraea* forereef. *L. apodus* and *H. flavolineatum* biomasses were significantly enriched in patch reef and shallow forereefs but not in the outer *Montastraea* reef.

Mangroves may enhance adult fish biomass in two ways. First, efflux of detritus and nutrients may enrich primary production in neighbouring ecosystems; however, this hypothesis is not well supported¹². Second, mangrove nurseries may provide a refuge from predators and/or plentiful food that increases the survivorship of juveniles¹³. Our data, although not constituting proof, support the latter hypothesis. For example, the size–frequency distribution of *H. sciurus* suggests an ontogenetic shift in habitat use from seagrass, to mangroves, to patch reefs, and finally to forereefs, their main adult habitat (Fig. 2). Our data suggest that juvenile grunts migrate from seagrass beds when they reach a length of 4–6 cm.

Migration occurs from seagrass to mangroves, but if mangroves are absent the grunts move to reefs (Fig. 2). Because mangroves offer refuge¹³ and the biomass of haemulid predators is greater on reefs than in mangroves (30 t km⁻² versus 18 t km⁻²; *t*-test, *P* < 0.05), the chances of grunt survival may be lower if grunts migrate directly to reefs. In short, some fish species move to their adult habitat in stages. As the biomass of predators increases at each stage, it is desirable to grow as large as possible before taking the next step towards adult habitat. We suggest that mangroves provide an intermediate nursery stage between seagrass beds and patch reefs, and they therefore alleviate a predatory bottleneck in early demersal ontogeny. For further details see Supplementary Information.

Large-scale ecological studies of pattern should infer causation only if alternative causative mechanisms have been tested and falsified¹⁴. Thus, we can only infer that mangroves enrich reef fish communities once plausible alternative explanations, such as variations in fishing intensity, have been discounted. There seemed to be four plausible alternative scenarios, each of which was tested and discounted (Table 2). Indeed, the pattern of direct fishing pressure tended to strengthen our conclusions: lutjanid biomasses were greater in mangrove-rich areas despite higher fishing pressure (Table 2). Therefore, either fishing of lutjanids is not particularly intense or we have underestimated the potential biomass enrichment of lutjanids by mangroves.

None of the 44 fish species that we encountered in mangroves was confined to that habitat and 37 (84%) were seen on *Montastraea* reefs as reproductively capable adults. However, juveniles of one reef

Table 1 Impact of extensive mangroves on the biomass of fish in patch reef, shallow forereef and *Montastraea* reef habitats

Species	Mean (s.e.m.) biomass (kg km ⁻²)											
	Patch reef				Shallow forereef				<i>Montastraea</i> reef			
	Scarce mangroves	Rich mangroves	Sig. factors*§	Biomass increase	Scarce mangroves	Rich mangroves	Sig. factors*	Biomass increase	Scarce mangroves	Rich mangroves	Sig. factors*	Biomass increase
<i>S. iserti</i>	–	–	–	–	–	–	–	–	1,530 (118)	2,170 (111)	M‡	42%
<i>H. sciurus</i>	1,205 (329)	33,349 (9,274)	M	2667%	56 (38)	425 (120)	M	659%	288 (53)	447 (55)	M, R	55%
<i>H. flavolineatum</i>	5,256 (1,460)	15,307 (4,114)	M, R	191%	516 (101)	1,600 (249)	M	210%	1,398 (149)	1,643 (139)	NS	–
<i>H. plumieri</i>	5,174 (1,614)	16,280 (3,591)	M	214%	317 (72)	843 (304)	M	165%	523 (62)	863 (69)	M	65%
Haemulidae¶	11,636 (2,089)	67,370 (12,971)	M, R	478%	889 (152)	3,031 (497)	M	240%	2,288 (188)	3,210 (192)	M, R, S‡	40%
<i>O. chrysurus</i>	769 (441)	410 (95)	R†	–	659 (150)	892 (187)	NS	–	3,098 (486)	6,715 (1,323)	M, S‡	116%
<i>L. apodus</i>	739 (354)	6,192 (1,566)	M	737%	622 (336)	2,392 (722)	M	284%	1,767 (226)	1,898 (259)	S‡	–
Lutjanidae¶	2,890 (1,228)	16,707 (4,805)	M	478%	1,882 (745)	4,428 (1,055)	M	135%	5,883 (796)	12,223 (1,503)	M, S‡	107%

The importance of mangroves and reef system in explaining patterns of biomass was tested by nested general linear model ANOVA. Data were transformed by the Box–Cox method. NS, not significant. *Significant factors (*P* < 0.05) are mangrove (M), reef system (R) and site (S). Where mangroves exerted significant influence, the increase in mean biomass is expressed as a percentage of the level in mangrove-scarce systems. Neither the biomass nor the density of any species in seagrass beds differed significantly between mangrove-rich and mangrove-scarce systems.

†The fit by the Box–Cox method was poor (*P* > 0.02), and the significance of mangroves could not be tested.

‡Site was only entered into these tests because site-level data (individual transects) often had to be pooled to increase sample size.

§Patch reef area was entered as a covariate for patch reefs but the slopes did not differ from zero.

¶*S. iserti* was not surveyed on patch reefs or shallow forereefs.

¶ All species in the family were assessed, not just those shown in the table.

Table 2 Alternative explanations of increased biomass observed in some haemulids, scarids and lutjanids in *Montastraea* reefs adjacent to rich mangroves

Potential alternative explanation of results	Test	Result	Decision
Direct fishing pressure: greater fishing pressure on haemulids and lutjanids in <i>M</i> _{scarce} systems	Compare density of artisanal and commercial fishers between <i>M</i> _{rich} and <i>M</i> _{scarce} systems*	Greater in all <i>M</i> _{rich} systems (J. Azueta, personal communication)	Reject
Indirect fishing pressure: fishing led to fewer predators of haemulids and lutjanids in <i>M</i> _{rich} systems	ANOVA of piscivore biomass between <i>M</i> _{rich} and <i>M</i> _{scarce} systems	No difference (10.5 ± 2.9 tonnes km ⁻² versus 10.1 ± 1.6 t km ⁻² ; mean ± s.e.m.)	Reject
Subtleties in habitat type: structure of reef habitat differs between <i>M</i> _{rich} and <i>M</i> _{scarce} systems	Nested ANOSIM of habitat composition and rugosity variables <i>M</i> _{rich} versus <i>M</i> _{scarce}	No difference (<i>P</i> > 0.05)	Reject
Internal validity of design: combination of barrier reef and atoll systems for <i>M</i> _{rich} treatment caused bias	Compare barrier and atoll systems for community structure and focal species biomass (evidence of bias), benthic structure (δ habitat), density of early haemulids in seagrass (δ recruitment)	Data do not group into barrier and atoll categories. All nested ANOVAs and ANOSIMs not significant (<i>P</i> > 0.05). Mean haemulid densities 78 ha ⁻¹ and 79 ha ⁻¹ in atoll and barrier seagrass	Reject

Most of these analyses focus on the *Montastraea* habitat, which, being most distant from mangroves, is perhaps most likely to be confounded by other factors. M represents the factor Mangrove entered into the analysis. δ denotes 'difference'.

*Fisheries statistics are currently being collated by J. Azueta (Fisheries Department, Belize), but the differences between *M*_{rich} and *M*_{scarce} reef systems are unequivocal and relate to the distribution of inhabited islands, fishing camps and proximity to fish markets.

species, the rainbow parrotfish *S. guacamaia*, were found exclusively in mangroves. *S. guacamaia* is the largest herbivorous marine fish in the Atlantic¹⁵ (reaching 1.2 m in length) and is listed as vulnerable on the IUCN *Red List of Threatened Species*¹⁶. Rates of encounter of *S. guacamaia* juveniles were very significantly greater in mangroves than in any other habitat ($P < 0.0001$), and we conclude that they are dependent on mangroves. This is consistent with limited reports indicating that *S. guacamaia* juveniles are usually seen in mangroves^{15,17}. If juveniles are mangrove dependent, we would expect adult *S. guacamaia* to be scarce or absent on reefs with little access to mangroves. This was found to be true: adult densities of *S. guacamaia* were strongly and significantly ($P < 0.0001$) enhanced on reefs near mangroves (see Supplementary Information).

Such functional dependency means that *S. guacamaia* is vulnerable to local extinction from habitat loss as well as from overfishing. Indeed, anecdotal information from Glovers Reef (D. Wesby, personal communication) suggests that *S. guacamaia* has undergone local extinction in the past 30 yr. Schools of this parrotfish were commonly observed in the 1960s when several of the islands had well-developed mangrove habitats. Unlike other study sites, all functional mangrove was cleared in the late 1960s and early 1970s, and in the mid- to late 1970s *S. guacamaia* was heavily fished. *S. guacamaia* is no longer fished and either has recovered or has survived at low densities at mangrove-rich sites. Its extinction at Glovers Reef seems most probably due to the removal of its nursery habitat.

The impact of historical overfishing on modern reef ecosystems has been discussed at length¹⁸. Reductions in herbivory may reduce the resilience¹⁹ of coral reefs to algal overgrowth. In the case of *S. guacamaia*, historical overfishing and mangrove deforestation may have worked synergistically to reduce herbivory and secondary production on many Caribbean coral reefs. We estimate that loss of a single adult *S. guacamaia* would constitute a 10% reduction in total parrotfish biomass within its territory (see Supplementary Information).

Extensive mangrove habitats can enhance the biomass of fishes on Caribbean reefs because tropical coastal ecosystems are functionally linked. Although precise corridors of connectivity between habitats are not fully understood as yet, the results have an important implication for conservation planning: management schemes should explicitly protect swaths of connected habitats rather than simply identify representative areas of each habitat in isolation²⁰. Given the ever-increasing range and severity of natural and anthropogenic disturbances to coral reefs²¹, any natural source of ecosystem production and resilience should be conserved. Our data suggest that the current rate of mangrove deforestation, which is greatest in the Americas at $2,251 \text{ km}^2 \text{ yr}^{-1}$ and exceeds that of tropical rainforests¹, will have significant deleterious consequences for the functioning, fisheries, biodiversity and resilience of Caribbean coral reefs. □

Methods

Fish and benthic surveys

Montastraea reefs were surveyed at a depth of 9–12 m, just inside the reef escarpment. All but nocturnal (such as Apogonidae) and highly cryptic (such as Clinidae and Gobiidae) fish species were surveyed by using discrete group visual fish census²². Those species were also ignored in other comparable studies²³. Species were divided into four groups, and their density and size (to the nearest centimetre) were estimated along belt transects by the same person at each site. Surveys were carried out at 09:00, 12:00 and 15:00 without systematic bias per site.

Transect size and number were optimized by using species-area curves from pilot surveys at Glovers Reef, which had relatively low fish density. The transect dimensions and numbers (given in parentheses) at each site were $30 \times 2 \text{ m}$ (6) for smaller benthic species; $30 \times 4 \text{ m}$ (10) for scarids, acanthurids, pomacanthids, diodontids and monacanthids; $100 \times 4 \text{ m}$ (6) for haemulids, chaetodontids, small serranids and labrids; and $100 \times 6 \text{ m}$ (6) for lutjanids, carangids, planktivorous labrids, large serranids and other large predators. Lutjanids and haemulids were surveyed on the shallow forereef by using $150 \times 4 \text{ m}$ (6) transects and on patch reefs by using $10 \times 4 \text{ m}$ (4) transects. We surveyed seagrass beds by using $50 \times 2 \text{ m}$ (12) transects and mangrove fringes by using $20 \times 2 \text{ m}$ (10) transects, of which less than a metre extended outside prop roots.

Fish lengths were converted to biomass by using allometric relationships²⁴. The percentage cover of coral, macroalgae, turf algae, coralline red algae and sand was measured in fifteen 0.25-m^2 quadrats per site. As an index of structural complexity, we measured the horizontal distance covered by a 2-m chain (0.3-cm links) draped tightly across the seabed ($n = 10$ per site). All surveys were completed during May and June 2002.

Calculation of predator biomass and statistical analysis

Previous studies have found that the main predators of haemulids and smaller lutjanids are *Sphyrna barracuda*, large lutjanids (such as *L. jocu*) and serranids (such as *Mycteroperca bonaci*) and carangids (such as *Caranx hippos*). We pooled biomass data for these groups to obtain a proxy for predation, which we tested by nested general linear model analysis of variance (ANOVA; site nested within reef, reef nested within mangrove extent).

Observations of uncommon species such as *S. guacamaia* cannot be analysed by conventional statistical methods, so we used bayesian methods based on the number of observations rather than fish densities (see Supplementary Information). Data were pooled from all six reef systems surveyed.

Received 8 August; accepted 9 December 2003; doi:10.1038/nature02286.

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Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements We thank T. Green for help with the online figures; B. Cowen, J. Pandolfi, S. Palumbi, D. Snyder, F. Micheli, B. Brown and J. Bythell for comments on the manuscript. We thank the National Geographic Society, the US World Wildlife Fund (WWF-US) and The Royal Society for funding. Field work was supported in part by the Lighthouse Reef Resort.

Competing interests statement The authors declare that they have no competing financial interests.

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